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Published in:
American Naturalist

DOI:
10.1086/663194

E-Article

The Forms and Fitness Cost of Senescence: Age-Specific Recapture, Survival, Reproduction, and Reproductive Value in a Wild Bird Population

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Submitted January 31, 2011; Accepted September 6, 2011; Electronically published November 22, 2011

Online enhancement: appendix.

abstract: Longitudinal studies of senescence accumulate rapidly from natural populations. However, it is largely unknown whether different fitness components senesce in parallel, how reproductive and survival senescence contribute to declines in reproductive value, and how large the fitness cost of senescence is (the difference between the observed reproductive value and the hypothetical reproductive value, if senescence would not occur). We analyzed age-specific survival in great tits *Parus major* and combined our results with analyses of reproductive senescence to address these issues. Recapture probability of breeding females declined with age, suggesting age-specific increases in skipped or failed breeding and highlighting an important bias that studies of senescence in wild populations should incorporate. Survival probability also declined with age and in parallel with recruit production. Reproductive value decreased 87% between age 1 and age 9 but at a fitness cost of only 4%; the proportion of the contribution of reproductive senescence versus survival senescence to this cost was 0.7. For 11 other species, we estimated fitness costs of senescence of 6%–63% (average: birds, 9%; mammals, 42%), with relative contributions of reproductive senescence of 0.0–0.7 (average: birds, 0.4; mammals, 0.3). We suggest that understanding when and why reproductive and survival senescence differ will help in the identification of proximate mechanisms underlying variation in rates of senescence and its evolution.

Keywords: age-specific reproduction and survival, reproductive value, senescence, life history, *Parus major*, mark-recapture models.

Introduction

Senescence is a late-life decline in organismal performance, thought to have evolved because unavoidable mortality reduces the number of individuals alive at old age, thereby weakening the force of natural selection (Fisher 1930; Medawar 1952; Williams 1957; Hamilton 1966). Reported late-life changes in performance are manifold and include changes in behavior (Catry et al. 2006; Lecomte et al. 2010), physiology (Angelier et al. 2007; Palacios et al. 2007; Moe et al. 2009; Broggi et al. 2010), and ornamentation (Galvan and Møller 2009; Evans et al. 2011). The evolutionary implications of late-life performance changes, however, depend on how such changes translate into age specificity of the two major fitness components: reproduction and survival. More specifically, in a stationary population these implications depend on the product of reproductive success and survival, captured in Fisher's (1930) reproductive value (Partridge and Barton 1996). Despite a recent resurgence of interest in the evolutionary ecology of senescence (Monaghan et al. 2008), the total impact of senescence, as measured using the age-specific decline in reproductive value, has been reported for very few species (Newton and Rothery 1997; Møller and de Lope 1999; Bonduriansky and Brassil 2002; Keller et al. 2008; Brown and Roth 2009).

Besides being combined to obtain an integrated measure of senescence, age-specific estimates of reproduction and survival can be used to compare the trajectory of senescence between these fitness components. If reproductive performance and survival probability senesce in parallel, then, at the proximate level, senescence may be expected to be the result of deterioration of aspects of bodily functioning that affect survival and reproduction equally (Williams 1957). However, since selection intensity on age-specific reproductive performance depends on the probability of reaching a certain age, while that on survival depends on future loss by death at that same certain age,

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Am. Nat. 2012. Vol. 179, pp. E15–E27. 0003-0147/2012/17901-52787$15.00.
DOI: 10.1086/663194

their patterns of late-life deterioration may not have necessarily evolved to be the same (Partridge and Barton 1996). While interspecific variation in the rate (Jones et al. 2008) and age at onset (Péron et al. 2010) of senescence is increasingly well understood, intraspecific variation in senescence trajectory between fitness components has received little attention. Indeed, understanding when and why senescence trajectories vary between life-history traits was recently identified as a key challenge in the study of senescence (Burger and Promislow 2006; Nussey et al. 2008).

Following a handful of studies under laboratory conditions, which suggest that rates of senescence differ between traits (e.g., Burger and Promislow 2006; Rueppell et al. 2007), a first observation of this phenomenon under natural conditions was made for red deer *Cervus elaphus*, in which male annual survival, breeding success, and antler mass showed very different patterns of age-related change (fig. 2 in Nussey et al. 2008). Rates of senescence were also found to differ among reproductive traits between, as well as within, males and females of that species (Nussey et al. 2009). In collared flycatchers *Ficedula albicollis*, female life-history traits and male ornaments show different age-trajectories, too (Evans et al. 2011). In addition, we showed recently, in a population of great tits *Parus major*, that the onset of female reproductive senescence advances and its rate becomes steeper over the course of successive reproductive stages within a breeding attempt (Bouwhuis et al. 2009). Specifically, we showed that females do not lay fewer eggs with advancing age but do undergo an age-specific decline in the number of chicks hatched from these eggs and the number of chicks reared to fledging. Senescence in number of chicks reared preceded that in number of chicks hatched by 1 year and contributed more strongly to overall age-specific deterioration in the number of local recruits produced (Bouwhuis et al. 2009). Since in most bird species the energetic costs of chick rearing exceed those of incubation (for a review, see Tatner and Bryant 1993), this observation could be interpreted as suggesting that within species, senescence may be determined by lowering of the energetic ceiling (Drent and Daan 1980) with age. Additional studies comparing the age-specific changes in multiple traits may suggest similar hypotheses as to the proximate origin of senescence effects.

Finally, knowledge of patterns of both age-specific reproductive performance and survival probability can be used to assess their relative contribution to the fitness cost of senescence, which we define as the difference between the observed reproductive value at the onset of reproduction and the hypothetical reproductive value if senescence were not to occur (following Bonduriansky and Brassil 2002). In a recent review, it was shown that for mammals, the fitness component most affected by the cost of reproduction varies with life span, such that in short-lived species in which fitness depends most on current reproduction and in which canalization is therefore expected to act against environmental variability in reproduction (Gaillard and Yoccoz 2003), costs of reproduction are more likely to be found in survival than in reproduction (Hamel et al. 2010). The relative contribution of declines in age-specific reproduction and survival to the fitness cost of senescence may similarly vary with life span, such that in short-lived species, stronger canalization against variability in reproduction causes fitness costs of senescence to be more likely to be found for survival than reproductive senescence, whereas the reverse holds true for long-lived species. Environmental canalization is, however, unlikely to prevent senescence, and since risk-prone strategies are expected to increase in frequency with age (Hamilton 1966), costs of reproductive senescence may still outweigh those of survival senescence in short-lived species and vice versa in long-lived species. This latter idea seems more likely in our short-lived study species, the great tit, since we have previously found costs of early-life reproduction on rates of reproductive senescence but not on reproductive life span (Bouwhuis et al. 2010*a*). The single previous study we are aware of that investigated the relative contribution of reproductive and survival senescence to the decline in reproductive value with age reported that males of the short-lived antler fly *Protopiophila litigata* lost 1.7 times more fitness due to declining reproductive performance than due to declining survival probability with age (Bonduriansky and Brassil 2002). This finding fits better with our prediction for the great tit than with the general prediction based on costs of reproduction in mammals, but replicate studies are clearly needed to shed light on the generality of this finding and to guide the development of theory regarding the relative contributions of reproductive and survival senescence to the fitness cost of senescence.

Here, we present data on age-specific survival in female great tits, for which we have recently shown reproductive senescence to occur (Bouwhuis et al. 2009). We combine survival and reproductive performance data to assess the age specificity of reproductive value and test whether age-specific declines in reproductive performance and survival probability are correlated. We further use these data to quantify the fitness cost of senescence and the relative contribution of reproductive and survival senescence to this cost. Last, we repeat these calculations for 11 other vertebrate species for which the necessary data have been published, for a preliminary assessment of the generality of our findings, and to test whether senescence patterns vary with life span.

Material and Methods

Study Population and Data Collection

Data used here come from a long-term study of great tits breeding in nest boxes in the ~380-ha mixed deciduous woodland of Wytham Woods, Oxfordshire, United Kingdom. The first nest boxes in this population were put up in 1947, but the number of boxes available for great tits has been approximately constant at 1,020 from 1960 onward. Each breeding season, nest boxes were checked at least weekly to collect basic breeding information. Chicks were ringed when 2 weeks old, and parents were trapped at the nest while feeding their chicks. Parental age was based on birth year for locally born birds or plumage characteristics (Svensson 1994) at first encounter for immigrants. Immigrants constitute, on average, 47% of the breeding population (McCleery et al. 2004), but most entered the population as yearlings, such that exact age was known for 92% of birds. For birds first encountered with adult plumage (which therefore were of unknown age), a minimal age of 2 was assumed. These birds were distributed among all age classes (fig. A1, available online). Only birds found breeding at least once were included in our sample.

Data Selection and Survival Analyses

Previous analyses of age-specific reproduction in our population (Bouwhuis et al. 2009) focused on females of known reproductive life span, because data on male reproductive performance are less complete and potentially confounded by extrapair paternity and reproductive life span is an important factor to include in models aiming to estimate within-individual patterns of a dependent variable with age (van de Pol and Verhulst 2006). These data comprised 4,935 individual females, whose breeding age ranged from 1 to 9, averaging 1.8 years.

For the survival analyses we constructed capture-recapture histories for the same sample of females. Encounter histories noted for each of the 47 breeding seasons in our data set (1960–2006) whether females were observed breeding (1) or not observed breeding (0). Goodness-of-fit tests on raw histories were performed to test for transience (i.e., single capture because of nomadic behavior or a short life span) and trap dependence (i.e., variation in recapture probability depending on the trapping history), using U-CARE 2.3 (Choquet et al. 2009*b*). The transience tests, assessing the null hypotheses of previously and newly ringed females being equally likely to be reencountered (called 3.SR: $\chi^2_{45} = 60.937$, $P = .057$) and the time until reencounter not being different for previously and newly ringed females (called 3.SM: $\chi^2_{44} = 33.161$, $P = .884$), were not statistically significant, and the trend toward previously ringed females being less likely to be reencountered than newly ringed females (i.e., the opposite of transience; estimate, -1.018) in test 3.SR may largely be explained by the age effects we were aiming to model. The tests of trap dependence, assessing the null hypotheses of no difference in reencounter probability between females trapped and not trapped at a previous occasion, given that they are alive (called 2.CT: $\chi^2_{43} = 37.299$, $P = .716$), and of no difference in the time until reencounter between females trapped and not trapped at a previous occasion (called 2.CL: $\chi^2_{16} = 11.499$, $P = .777$), were also not statistically significant. We therefore used the Cormack-Jolly-Seber model as a starting point for model selection (Lebreton et al. 2009).

Previous analyses of recapture and survival probabilities in our study population have revealed recapture probability to be higher but survival probability to be slightly lower in locally born females compared to immigrants (Clobert et al. 1988). We therefore defined the following three states: alive as a locally born female; alive as an immigrant female; or dead, which could probabilistically be inferred from three events: observed as a locally born female, observed as an immigrant female, or not observed. Transition was allowed only between being alive and being dead but not between being locally born and being immigrant. We analyzed these data by using multistate capture-recapture models (Clobert et al. 1987; Lebreton et al. 2009) implemented in the programme E-SURGE 1.6.0 (Choquet et al. 2009*a*). While fixing survival probability to vary with immigrant status and age, we first modeled recapture probability (p), which was allowed to vary with time, age, and female immigrant status (table 1, step 1). The four best-supported models were then used to model local survival probability (Φ), which was also allowed to vary with time, age, and female immigrant status (table 1, step 2). In these models, age was considered either a class variable (a) or a covariate (age and age^2, found to best describe reproductive aging in our population; Bouwhuis et al. 2009), while we also fitted Gompertz and two-parameter Weibull models, which have been shown to best describe aging patterns in populations of large mammals (Gaillard et al. 2004). Time and age effects were considered additive (i.e., average age-specific survival was allowed to vary between years, but the rate of actuarial aging was not), whereas we tested for both additive (intercept) and multiplicative (slope) effects of immigrant status. Models were compared and ranked on the basis of a quasi Akaike Information Criterion (qAIC; Burnham and Anderson 2002), calculated as qAIC = [(deviance/overdispersion parameter $\hat{c}$) + 2 × number of parameters estimated].

Table 1: Model selection results for age effects on local survival (Φ) and recapture probability (p) in 4,935 female great tits

Step, model	Φ	p	No. estimated parameters	Deviance	ΔqAIC
1:					
1	Status × a	**Status + age + t**	67	19,384.340	.000
2	Status × a	**Age + t**	66	19,386.544	.171
3	Status × a	**Status + age^2 + t**	68	19,384.214	.762
4	Status × a	**Age^2 + t**	67	19,386.422	.970
5	Status × a	Status + t	66	19,391.706	5.333
6	Status × a	t	65	19,394.228	5.823
7	Status × a	a + t	73	19,382.884	9.432
8	Status × a	Status + a + t	74	19,380.894	9.442
9	Status × a	Status × (age + t)	113	19,334.431	40.979
10	Status × a	Status × t	111	19,341.334	46.932
11	Status × a	Status × (age^2 + t)	115	19,334.345	48.168
12	Status × a	Status + age	22	19,532.066	56.737
13	Status × a	Status + age^2	23	19,532.034	58.582
14	Status × a	i	20	19,541.818	62.366
15	Status × a	Status	21	19,540.022	62.682
16	Status × a	Status × (a + t)	127	19,325.296	63.840
17	Status × a	a	28	19,530.528	67.273
18	Status × a	Status + a	29	19,529.365	68.124
19	Status × a	Age^2	21	19,546.136	68.684
20	Status × a	Status × age^2	23	19,550.765	77.447
21	Status × a	Status × age	21	19,555.033	77.693
22	Status × a	Status × a	35	19,527.970	78.824
23	Status × a	Age	20	19,563.199	83.747
2:					
1	**Gompertz + t**	**Status + age + t**	98	19,166.373	.000
2	**Age^2 + t**	**Status + age + t**	97	19,168.634	.261
3	**Weibull + t**	**Status + age + t**	98	19,166.858	.485
4	Status + Gompertz + t	Status + age + t	99	19,166.373	2.000
5	Status + age^2 + t	Status + age + t	98	19,168.634	2.261
6	Status + Weibull + t	Status + age + t	99	19,166.858	2.485
7	a + t	Status + age + t	103	19,165.613	11.865
8	Status + a + t	Status + age + t	104	19,165.613	13.917
9	Age + t	Status + age + t	96	19,185.793	17.701
10	Status + age + t	Status + age + t	97	19,185.789	19.744
11	t	Status + age + t	95	19,198.555	26.182
12	Status + t	Status + age + t	96	19,198.538	30.446
13	Status × (age^2 + t)	Status + age + t	145	19,124.901	52.528
14	Status × (a + t)	Status + age + t	157	19,100.139	57.887
15	Status × (age + t)	Status + age + t	143	19,142.877	71.576
16	Status × t	Status + age + t	141	19,156.282	80.840
17	Gompertz	Status + age + t	53	19,409.143	152.770
18	Status + age^2	Status + age + t	53	19,409.228	153.552
19	Status + Gompertz	Status + age + t	54	19,408.293	153.921
20	Status × a	Status + age + t	67	19,384.340	157.079
21	a	Status + age + t	58	19,406.391	160.018
22	Weibull	Status + age + t	53	19,417.363	160.990
23	Status + a	Status + age + t	59	19,405.599	161.226
24	Status + age	Status + age + t	52	19,427.509	169.808
25	i	Status + age + t	50	19,439.644	177.271
26	Status	Status + age + t	51	19,439.095	178.722
27	Status + Weibull	Status + age + t	54	19,438.999	184.627
28	Age	Status + age + t	20	19,448.770	187.018
29	Age^2	Status + age + t	51	19,448.492	188.765
30	Status × age	Status + age + t	51	19,448.624	188.897
31	Status × age^2	Status + age + t	53	19,447.247	191.571

Note: Best-supported models are presented in bold. For each model, the number of estimated parameters is shown, along with the deviance and the difference in quasi Akaike Information Criterion (ΔqAIC) between that model and the best-supported model. In the model description, i indicates constant recapture or survival, status immigrant status (i.e., locally born versus immigrant), t time (i.e., year effects), a age as a class variable, and age/age^2 age as a covariate.

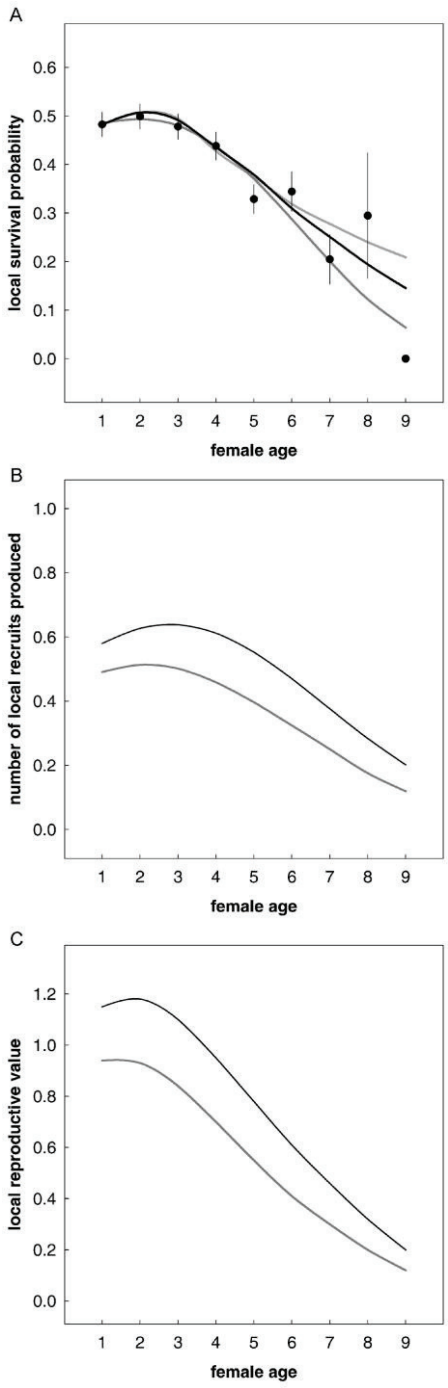

Figure 1: Age-specific performance in 4,935 female great tits. *A*, Local survival probability, where fitted curves represent age-specific survival calculated from the three best-supported models (table 1; black line = Gompertz; dark gray line = age^2; light gray line = Weibull) and the filled circles represent average ± SE survival probability at each age when fitting age as a class variable (table 1, step 2, model 7). *B*, Local recruit production, where the black line is calculated using the model describing within-individual age-specific recruit production reported by Bouwhuis et al. (2009) and the gray line corrects for declining recapture probability with age, assuming that a failure to catch the female is due to skipped or failed breeding. *C*, Reproductive value, calculated by combining the model-averaged age-specific survival probability from the three best survival models (table 1, step 2, models 1–3) and both estimates of local recruit production.

Reproductive Value

Female age-specific reproductive values were calculated following Newton and Rothery (1997), using the average age-specific survival probabilities as estimated by the best-supported survival model (fig. 1*A*, black line) and the within-individual fitted curve of local recruit production based on females of the average reproductive life span of 1.8 years (fig. 1*B*). At age *a*, the expected number of local recruits produced from reproduction at age *a* until age at last reproduction (i.e., 9 years in our study) in a stationary population is given by

$$\mathrm{RV}_a = \sum_{x=a}^{\mathrm{ALR}} \frac{l_x}{l_a} m_x,$$

where RV is reproductive value, ALR is age at last reproduction, l_x is the probability of a female surviving to age x, and m_x is the average number of local recruits produced by a female of age x. The term l_x/l_a defines the probability of surviving to age x, given that the female has survived to age a. If s_x is the probability of survival from age x to age $x + 1$, then $l_x/l_a = s_a \times s_{a+1} \times \ldots \times s_{x-1}$.

Note that because our estimate of reproductive performance is based on local recruit production, which we know to be only part of the total recruit production due to emigration of offspring from Wytham to the surrounding areas (Verhulst et al. 1997), our estimate of reproductive value is also local. However, since we have no evidence that emigration of offspring varies with maternal age (Bouwhuis et al. 2009), we do not expect a bias and consider it safe to assume that the decline in local reproductive value provides an unbiased index of the decline in the true reproductive value. Moreover, we have shown lifetime reproductive success of recruited offspring to be independent of maternal age in our population (Bouwhuis et al. 2010*b*), such that our measure of reproductive value based on the number of recruits is an appropriate fitness measure.

Correlated Age Specificity of Reproduction and Survival

To test whether reproductive performance and survival probability senesce in parallel, we calculated the correla-

tion between their age-specific changes, using base values estimated from models that use age as a class variable.

Fitness Cost of Senescence

The fitness cost of senescence was calculated using the difference between the actual reproductive value observed at age 1 (when great tits are sexually mature) and the hypothetical reproductive value if senescence were not to occur (Bonduriansky and Brassil 2002). The latter was estimated by keeping both survival probability and local recruit production constant from the age of peak performance onward, that is, from age 2 in this population (Bouwhuis et al. 2009). Because the absence of survival senescence would cause more individuals to reach very old age, we extended the calculation of both the actual reproductive values and the hypothetical reproductive values to an age at last reproduction of 15 years, instead of 9, when even without survival senescence the probability of being alive would be $(0.49)^{14} = 0.00005$ and therefore have negligible effects on the reproductive value at age 1. The total cost of senescence was defined as $[(RV_{no\ S} - RV_{observed})/RV_{no\ S}) \times 100\%$, where the subscript "no S" indicates no senescence.

To assess the relative fitness cost of senescent declines in reproductive performance and survival probability with age, we calculated two other hypothetical reproductive values at age 1 by keeping either survival probability ($RV_{no\ SS}$, where the subscript "no SS" indicates no survival senescence) or local recruit production ($RV_{no\ RS}$, where the subscript "no RS" indicates no reproductive senescence) constant from the age of peak performance onward. We defined their relative contribution as

$$\frac{RV_{no\ RS} - RV_{observed}}{[(RV_{no\ RS} - RV_{observed}) + (RV_{no\ SS} - RV_{observed})]}.$$

A proportion larger than 0.5 would suggest reproductive senescence to be more costly than survival senescence, while a proportion smaller than 0.5 would indicate the opposite.

Results

Age-Specific Recapture and Survival Probabilities

Female recapture probability was best described to vary between years, to differ between locally born females and immigrant females, and to decline linearly with age (table 1, step 1, model 1). However, this model was not significantly better supported than the next three best models, which excluded the female immigrant status effect or included a quadratic effect of age (table 1, step 1, models 2–4). We therefore used all four supported recapture probabilities to model survival probability (table 1, step 2; table A1, steps 3–5, available online), and the best models (table 1, step 2, models 1–3) confirmed recapture probability to vary between years, to differ between locally born females and immigrant females, and to decline linearly with age. The immigrant status effect was, however, quite small, with recapture probability ranging from 0.86 ± 0.05 at age 1 to 0.62 ± 0.15 at age 9 for locally born females, the overall weighted average being 0.84 ± 0.06, while for immigrant females, recapture probability ranged from 0.83 ± 0.06 to 0.57 ± 0.15 between the ages of 1 and 9, with an overall weighted average of 0.81 ± 0.07. The overall average recapture probability was 0.83 ± 0.07.

Female local survival varied in level between years, and the best-supported models also included an effect of age (table 1, step 2, models 1–3). The age effect was equally well described by a Gompertz, Weibull, or age^2 function (fig. 1*A*), and we used model-averaged values from these three models in further calculations. Overall, average survival probability was 0.48 ± 0.05, but age-specific values ranged from 0.50 ± 0.05 at age 2 to 0.14 ± 0.04 at age 9 (table A2, available online). The next best-supported models (table 1, step 2, models 4–6) also included an additive effect of female immigrant status, but survival probabilities of locally born and immigrant females differed only at the fourth digit (data not shown), such that there is no biological relevance of this effect.

Age-Specific Reproductive Value

Combining age-specific local survival probability with age-specific local recruit production, as estimated for females of the average longevity of 1.8 years (fig. 1*B*, black line) from Bouwhuis et al. (2009), showed that reproductive value in female great tits depended strongly on age. It slightly increased (by 0.03 expected recruits, 3%) from age 1 to age 2, before declining (by 0.98 expected recruits, 83%) between the ages of 2 and 9 (fig. 1*C*, black line).

Note that the calculation of the age-specific reproductive values reported above is based on previously published estimates of local recruit production (Bouwhuis et al. 2009), which did not take into account a decline in female recapture probability with age, as documented in this study. Failure to catch females who are actually alive can arise from multiple sources. First, females could become increasingly trap shy with age while still breeding successfully. However, the absence of evidence for trap dependence in our data (see "Material and Methods") does not suggest this to be a likely scenario, and even if this were to play a role, only 4% out of the 10% of breeding attempts in our long-term study for which no female was caught produced fledglings. Of these successful breeding attempts, only one-third resulted in the production of one

to four local recruits. Second, breeding attempts could have failed before the female could be caught (6% of all breeding attempts in the long-term study), or females might have skipped reproduction because of poor environmental or individual conditions (e.g., Dhondt 1985). In this case, no recruits would have been produced. Finally, females could have bred in natural cavities or outside the study area, but the available evidence suggests the frequency of such attempts to be extremely low (Harvey et al. 1979; Perrins 1979), and it is not clear why this would be more frequent at old age. Unfortunately, we have no way to assess the frequency of these causes, but skipped and failed breeding seem to be especially likely to underlie the decline in female recapture probability with age. If this is the case, we underestimated the rate of reproductive senescence and thus biased our estimates of age-specific reproductive values. We therefore used the average age-specific recapture probability (table A2) and multiplied it by the age-specific local recruit production of identified females to calculate the maximum rate of reproductive senescence (fig. 1*B*, gray line) and reproductive value senescence (fig. 1*C*, gray line). We found that reproductive value peaks at 0.94 expected local recruits at age 1 before declining by 87% to 0.12 expected local recruits at age 9 (table A2). The onset of senescence, according to this estimate, therefore occurs 1 year earlier, and the proportional drop in reproductive value is 4% larger, as compared to calculations that ignored the declining capture probability with age. Moreover, the bias in the estimated reproductive values increases with age, from 1.22 at age 1 to 1.67 at age 9 (table A2).

Correlation, Cost, and Contribution

The correlation between the change in estimated local recruit production and change in survival probability between age 1 and age 8 was strongly positive at 0.847 (table 2). Taking into account the decline in recapture probability with age and using this to adjust values of age-specific local recruit production gave a similar result, with the correlation coefficient being 0.844 (table 2; fig. 2, open circles).

Excluding both reproductive senescence and survival senescence from the life history of the great tits increased their reproductive value at age 1 to 1.190. Compared to the expectation of 1.152 under observed levels of senescence, this entailed a rather small total fitness cost of 3.2% (table 2). Again, adjusting values of age-specific local recruit production based on age-specific recapture probabilities and assuming no capture to indicate zero recruit production resulted in the reproductive value at age 1 increasing from 0.943 to 0.984, such that the fitness cost of senescence was estimated at 4.2% (table 2).

To assess the relative fitness cost of senescent declines in reproductive performance and survival probability with age, we calculated the hypothetical reproductive values at age 1 by keeping either survival probability or local recruit production constant from the age of peak performance. The reproductive value when excluding only reproductive senescence was 1.165, while excluding only survival senescence resulted in a reproductive value of 1.167. The share of reproductive senescence in the cost of reproductive and survival senescence combined was therefore 0.464 (table 2). However, if we used local recruit production values corrected for age-specific recapture probabilities, the reproductive values while excluding only reproductive senescence or survival senescence, respectively, were 0.965 and 0.954. Given these predictions, the share of reproductive senescence relative to reproductive and survival senescence combined was 0.667 (table 2), and we believe the latter to be the more accurate estimate.

Interspecific Comparison

Among the 12 vertebrate species for which we obtained data, the correlation between age-specific declines in reproductive performance and survival probability varied from −0.23 to 0.99 (table 2). This correlation was strongly positive only in great tits, sparrowhawks *Accipiter nisus*, silvereyes *Zosterops lateralis chlorocephalus*, and soay sheep *Ovis aries*. There was no significant difference in the level of this correlation between birds and mammals (class: -0.098 ± 0.165, $\chi_1^2 = 0.353$, $P = .552$), but there was a strong negative relationship with maximum age-specific survival rate in both classes combined (peak survival rate: -1.715 ± 0.372, $\chi_1^2 = 21.242$, $P < .001$; fig. 3*A*).

The relative contribution of reproductive senescence to overall senescence was extremely variable between species, ranging from 0.015 in soay sheep to 0.672 in red deer (table 2). There was no clear difference between birds (average, 0.4) and mammals (average, 0.3) and no clear relationship with peak survival rate (fig. 3*B*).

Finally, the total fitness cost of senescence was strikingly different between birds (average cost, 9%; range, 4.5%–13.5%) and mammals (average cost, 42%; range, 9.7%–62.5%). The relationship between peak survival rate and the fitness cost of senescence was different between these classes as well (class × survival rate: $\chi_1^2 = 21.031$, $P < .001$), with a strong correlation between peak survival rate and the cost of senescence in mammals but no such pattern apparent in birds (fig. 3*C*). The lack of correlation between peak survival rate and the contribution of reproductive senescence to overall senescence (fig. 3*B*) suggests that the higher fitness costs of senescence in mammals with a high peak survival rate are not simply due to animals with high peak survival rates having more to lose.

Table 2: Costs and components of senescence across species

Species	Survival	Correlation	$RV_{age\ 1}$	$RV_{no\ RS}$	$RV_{no\ SS}$	$RV_{no\ S}$	$Ratio_{RS/SS}$	Cost	Source
Great tit (rec)[a,b]	.49	.847	1.152	1.165	1.167	1.190	.464	3.2	1
Great tit (rec_{min})[a,b]	.49	.844	.943	.965	.954	.984	.667	4.2	1
Great tit (fl_{min})[a,b]	.49	.916	10.942	11.115	11.080	11.342	.556	3.5	1
Sparrowhawk (fl)[c,d]	.66	.987	4.947	5.012	5.023	5.229	.461	5.4	2
Barn owl (fl)[a,e]	.81	.392	8.525	8.534	8.950	9.240	.021	7.7	3
Wood thrush (fl)[f,g]	.69	.381	5.602	5.734	5.695	6.139	.587	8.7	4
Song sparrow (fl)[b,f]	.60	.316	6.327	6.776	6.554	7.249	.664	12.7	5
Silvereye (fl)[g,h]	.65	.707	5.732	5.779	6.413	6.623	.065	13.5	6
Soay sheep (rec)[e,f]	.55	.796	.659	.660	.724	.730	.015	9.7	7
Red squirrel (wp)[a,e]	.75	.133	3.270	3.432	3.479	4.376	.437	25.3	8
Bighorn sheep, Ram Mountain (cp)[a,e]	.95	.378	5.491	5.719	6.821	9.849	.146	44.2	9, 10
Bighorn sheep, Sheep River (cp)[a,e]	.95	−.193	5.401	5.592	6.962	9.907	.109	45.5	9, 11
Red deer (cp)[a,b]	.96	.177	3.175	3.878	3.518	6.520	.672	51.3	12, 13
Roe deer (cp)[a,e]	.96	.187	6.544	7.200	8.525	15.783	.249	58.5	14, 15
Mountain goat (kp)[a,e]	.99	−.233	2.945	3.240	3.666	7.848	.290	62.5	16
Antler fly	...	...	...	...	...	...	...	20.0	17

Note: For great tits (this study) and 12 populations of 11 other species with published data on female age-specific recruit (rec), fledgling (fl), calf (cp), kid (kp), or weaned pup (wp) production and survival probability, we give (i) peak survival rate, (ii) the correlation coefficient between the age-specific change in reproductive performance and survival probability, (iii) the reproductive value at age 1 ($RV_{age\ 1}$), (iv) the hypothetical reproductive value when excluding reproductive senescence ($RV_{no\ RS}$), (v) the hypothetical reproductive value when excluding survival senescence ($RV_{no\ SS}$), (vi) the hypothetical reproductive value when excluding both reproductive and survival senescence ($RV_{no\ S}$), (vii) the relative contribution of reproductive senescence (vs. survival senescence) to overall senescence, and (viii) the total fitness cost (in percentage) of the observed rates of senescence. The subscript "min" shows that the calculation was based on values reported in Bouwhuis et al. (2009) corrected for the age-specific decline in recapture probability found in this study. Sources: 1, Bouwhuis et al. (2009); 2, Newton and Rothery (1997); 3, Altwegg et al. (2007); 4, Brown and Roth (2009); 5, Keller et al. (2008); 6, Knape et al. (2011); 7, Clutton-Brock and Pemberton (2004); 8, Descamps et al. (2008); 9, Loison et al. (1999); 10, Bérubé et al. (1999); 11, Festa-Bianchet and King (2007); 12, Catchpole et al. (2004); 13, Nussey et al. (2009); 14, Gaillard et al. (1993); 15, Gaillard et al. (2003); 16, Festa-Bianchet and Côté (2008); 17, Bonduriansky and Brassil (2002).

[a] Survival estimates come from a mark-recapture model in which age is fitted as a class variable.

[b] Reproductive success estimates come from a model that corrects for individual heterogeneity and in which age is fitted as a class variable.

[c] Survival estimates come from a mark-recapture model in which age is fitted as a continuous variable.

[d] Reproductive success estimates come from a model in which age is fitted as a continuous variable.

[e] Reproductive success estimates come from a model in which age is fitted as a class variable.

[f] Survival estimates come from a model in which age is fitted as a class variable.

[g] Reproductive success estimates come from a model that corrects for individual heterogeneity and in which age is fitted as a continuous variable.

[h] Survival estimates come from a model that corrects for individual heterogeneity and in which age is fitted as a continuous variable.

Discussion

Age-Specific Recapture and Local Survival

Female local survival probability was similar for locally born and immigrant female great tits and strongly age dependent, being 0.48 at age 1 and increasing to 0.50 at age 2 before diminishing by 72% to 0.14 at the age of 9, the maximum age recorded in the population. These findings largely agree with reports from previous analyses performed on a subset of the data, which also showed survival probability to vary quadratically with age (McCleery and Perrins 1989) and to be similar for locally born and immigrant females (Clobert et al. 1988). The overall survival rates reported by Clobert and colleagues (1988) of 0.40 for locally born females and 0.41 for immigrant females were, however, lower than our overall value of 0.48. This discrepancy may partly be explained by the fact that in the mid-1970s wooden nest boxes were gradually replaced by woodcrete nest boxes that render incubating females less prone to predation and hence cause higher overall survival probabilities (McCleery et al. 1996). The study by Clobert and colleagues (1988) was performed using data between 1964 and 1983, such that our data set included 23 extra years of higher survival probabilities. Moreover, Clobert et al. (1988) did not correct for age-specific recapture probabilities, which must have caused underestimation of survival rates.

We further found recapture probability to decline with age while varying between years and being slightly lower in immigrant females than in locally born females. The age-specific decline in recapture probability is likely to reflect females to be more prone to failing early in the breeding cycle and/or refraining from breeding completely with advancing age. Previous work on color-banded birds in a Belgian population of great tits has suggested that skipped breeding occurs in females after the age of 5, while

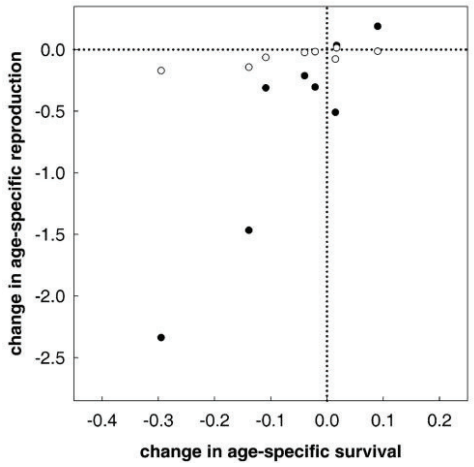

Figure 2: Correlations between the age-specific change in reproductive performance and survival probability in great tits. Open circles represent the relationship when using the minimum number of recruits produced in the analysis, while filled circles come from an analysis using the minimum number of fledglings as a measure for reproductive performance.

early breeding failure did not depend on female age (Dhondt 1985). If skipped breeding indeed underlies the age-specific decline in female recapture probability, this emphasizes the need to model age-specific recapture probabilities when aiming to test for the effects of age on local survival probabilities (also see Lebreton et al. 1992). In addition, it suggests that age-dependent declines in reproductive performance may be underestimated if changes in capture probability are not taken into account, and we here explored its consequences by assuming all failure to catch a female to have resulted in no recruit production. For the estimate of age-specific local recruit production, ignoring age-specific increases in what we assume to be early failure and/or skipped breeding led to an overestimation of recruit production of 18% at age 1 but of 68% at age 9 (table A2). This in turn had consequences for estimates of age specificity of reproductive value and the total fitness cost of senescence, which we will discuss below. We hope that other studies in which individuals can be identified earlier in the breeding cycle will provide more insight in the extent to which skipped breeding contributes to reproductive senescence.

Age-Specific Reproductive Values

Our finding of strong age dependence of survival probability adds to our finding of age dependence of reproductive performance (Bouwhuis et al. 2009; this study). It is therefore no surprise that a combination of these two traits in Fisher's (1930) reproductive value shows that total fitness, defined as the expected number of local recruits produced over the remaining reproductive life span, shows strong age specificity. Based on our previous estimate of reproductive senescence (Bouwhuis et al. 2009), reproductive value was found to decline 83% between the ages of 3 and 9, which, since we have previously shown that in any given year an average of 20% of breeding females is between 3 and 9 years of age (Bouwhuis et al. 2009, 2010*a*), shows that senescence is not only strong but also widespread. Based on the maximum rate of reproductive senescence, as estimated by taking into account the age-dependent decline in recapture probability we found here, total senescence effects are even more pronounced, with a decline in reproductive value of 87% between age 1 and age 9. The true extent of senescence is likely to lie somewhere between these two estimates, because a few of the females that were not captured may have bred successfully, but we expect it to be close to the second estimate.

Correlations and Fitness Costs

For most of the great tit's life, the age-specific changes in local recruit production and survival probability ran in parallel, as shown by the strong correlation between the changes from one age to the next in reproductive success and survival. This finding did not depend on whether we used estimates of age-specific recruit production that were or were not corrected for age-specific recapture probability of females. The fact that age-specific changes in both traits run in parallel may suggest a single process to underlie these patterns, and integrative work on physiological markers of aging (such as oxidative stress [Alonso-Alvarez et al. 2006], metabolic aging [Moe et al. 2009; Broggi et al. 2010], or telomere dynamics [Salomons et al. 2009]) and patterns of senescence as revealed in this study would facilitate our understanding of the mechanisms underlying the process of senescence. The correlation between age-specific changes in reproductive performance and survival probability was also high in sparrowhawks, silvereyes, and soay sheep. In sparrowhawks and silvereyes, this could be partly due to both traits being modeled using a similar age function, but for the great tits and soay sheep, age was modeled as a class variable, such that the positive correlation cannot be a statistical artifact. In the other eight vertebrate species, a correlation between the change in reproductive performance and survival from one age to the next was only slightly positive or even negative, suggesting that while one trait deteriorates, the other can remain at a similar level or improve. This could indicate that the mechanisms and/or aspects of phenotypic state causing reproductive and survival senescence are often decoupled, either because different aspects of state determine

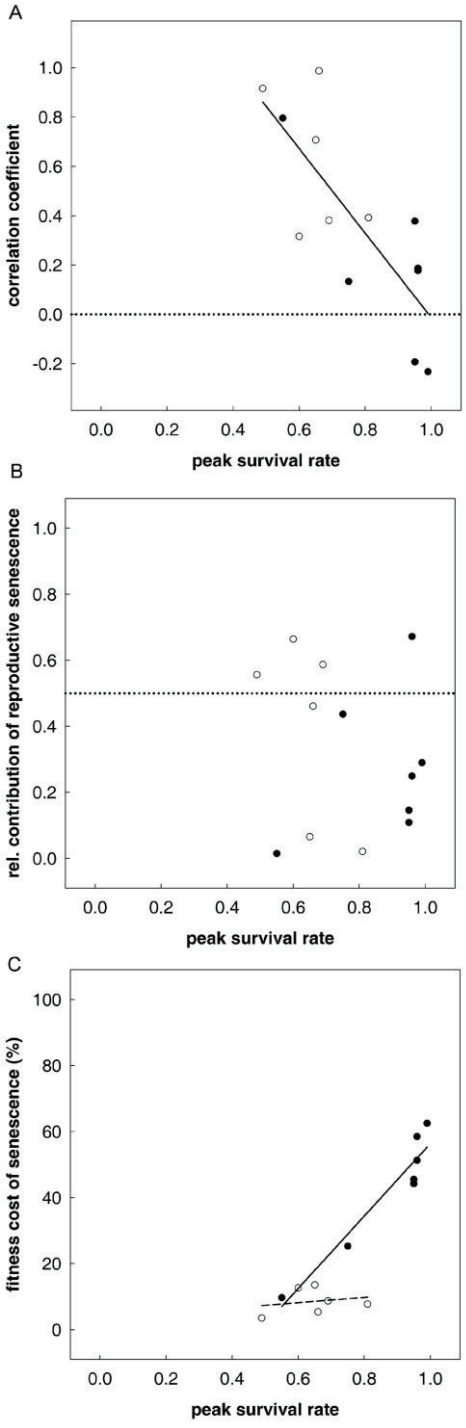

Figure 3: Interspecific comparison of (*A*) correlations between age-specific changes in reproduction and survival, (*B*) the relative contribution of reproductive senescence to overall senescence, and (*C*) the total fitness cost of senescence, in relation to peak survival rate. Open circles refer to avian studies in table 2, while filled circles represent the mammalian studies.

success at reproduction and survival or because the functions linking a critical aspect of state to performance differ between reproduction and survival. The strong negative relation between the species-level correlations and peak survival rates (fig. 3*A*) shows that such decoupling is especially likely in long-lived species.

Despite proceeding in parallel, our great tit data show senescence in recruit production to have a twofold larger fitness cost than survival senescence, with a ratio of 0.667. This larger cost of reproductive senescence may reflect the fact that the cost of reproduction comes in the form of accelerated reproductive senescence rather than in survival (Bouwhuis et al. 2010*a*) in our population. The ratio is close to that previously found in the short-lived antler fly, in which the fitness cost of reproductive senescence exceeded that of survival senescence by a factor of 1.7 (Bonduriansky and Brassil 2002). In comparison to other bird species, the Wytham great tits had the largest contribution of reproductive senescence to overall senescence, although the contribution included in this analysis was based on the number of fledglings produced and, at 0.556 (fig. 2, filled circles), was considerably lower than that based on the number of recruits produced. The lower value for the contribution based on the number of fledglings produced confirms our previous finding of only half of reproductive senescence being explained by the number of fledglings produced, while the other half is manifested between fledging and recruitment of offspring (Bouwhuis et al. 2009). If such underestimation of reproductive senescence while using short-term fitness measures is general, the potential conclusion of our interspecific comparison that, in most species, survival senescence is more detrimental to fitness than reproductive senescence should be interpreted with caution. Similarly, although we found no evidence for the predicted positive relation between peak survival rate and contribution, analyses of additional species and more fitness measures will be required before we can understand whether trait canalization can underlie the evolution of senescence, as it does the cost of reproduction (Hamel et al. 2010).

The total fitness cost of senescence in great tits, measured as a loss in reproductive value at age 1, was rather small: 4.2%. In the interspecific analysis, this cost ranged from 3.5% to 13.5% in birds (average, 9%) but was much higher in mammals, in which it ranged from 9.7% to 62.5% (average, 42%). The relationship between peak survival rate and the fitness cost of senescence was different between birds and mammals as well, with a larger cost of senescence in longer-lived mammals but no such pattern in birds. Although this difference fits well with findings of birds having slow rates of aging in comparison to mammals of the same size (Jones et al. 2008), our data set did not include birds of exceptionally long life span, and add-

ing such species will be crucial before the generality of the difference can be assessed.

Conclusions

Overall, our analyses have provided strong evidence for senescence in reproductive success, survival probability, and reproductive value in a wild bird population while also revealing that the anticipated fitness cost of senescence is rather low and dominated mostly by costs of reproductive senescence rather than survival senescence. Our interspecific comparison has shown that this finding may not be generalized to other species and that birds and mammals may show different costs and patterns of contribution of reproductive and survival senescence to overall senescence. We hope that these observations will inspire more extensive comparative work, as well as the development of a unifying theory of senescence (Gavrilov and Gavrilova 2005), which will include fitness costs of senescence and the contributions of reproduction and survival to these costs.

Acknowledgments

We gratefully acknowledge the many generations of Wytham field-workers without whom this study would not have been possible and thank the Natural Environment Research Council and the Biotechnology and Biological Sciences Research Council for grants and studentships funding the data collection. We would also like to thank R. Altwegg, S. Boutin, E. Catchpole, S. Descamps, and A. Roulin (the Kluane Red Squirrel project); P. Arcese, M. Festa-Bianchet, L. Keller, and J. Reid (the Mandarte project); and D. Nussey for providing us with the raw data on age-specific reproductive performance and survival probability for their study species. Moreover, constructive comments from D. Nussey and one anonymous reviewer greatly improved the manuscript. Collaborative work between S.B. and R.C. was funded by the school of Behavioural and Cognitive Neuroscience of the University of Groningen. S.B. and B.C.S. were supported by the European Research Council and S.V. by an NWO Vici grant from the Dutch Science Foundation.

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Associate Editor: Jean-Michel Gaillard
Editor: Mark A. McPeek

A female great tit incubating her clutch. Photograph by Sandra Bouwhuis.